

## **Spatio-temporal distribution of size classes and larval instars of aquatic insects (Ephemeroptera, Trichoptera and Lepidoptera) in a *Potamogeton pectinatus* L. bed (Lake Geneva, Switzerland)**

Ruth BÄNZIGER

Laboratoire d'écologie et de biologie aquatique, 18 ch. des Clochettes,  
University of Geneva, CH-1206 Geneva, Switzerland.

### **Spatio-temporal distribution of size classes and larval instars of aquatic insects in a *Potamogeton pectinatus* L. bed (Lake Geneva, Switzerland).**

Temporal changes of aquatic insect instars or size classes were monitored in different parts of a *Potamogeton pectinatus* bed. The hypothesis of a different distribution of the aquatic insects in the macrophyte bed according to their life stage and of a spatio-temporal segregation of congeneric species was tested. Head capsules widths of seven insect species (*Caenis horaria* and *C. luctuosa* (Ephemeroptera), *Mystacides azurea*, *M. longicornis*, *Oecetis lacustris* and *O. ochracea* (Trichoptera) and *Acentria ephemerella* (Lepidoptera)) were measured at monthly intervals from May to November 1994. Samples were taken in the edge and in the centre of the macrophyte bed on all sampling occasions, and in May, June and July, additional samples were taken from the 2 m sediment belt adjacent to the macrophyte bed. Each couple of congeneric species showed segregation by size before hibernation and showed delayed emergence patterns.

**Key-words:** Lake - Ephemeroptera - Trichoptera - Lepidoptera - macrophyte - distribution - size class.

## **INTRODUCTION**

Habitat segregation or space partitioning among closely related species have been often addressed in rivers (Malas & Wallace, 1977; McAuliffe, 1984). Few papers, however, have been concerned with this subject in lakes. Species with similar ecological niches are not always separated in space and time, thus competition is not necessarily involved and some congeneric species do coexist (Hildrew & Edington, 1979). Segregation, if there is any, is therefore likely to occur at another scale than at the species level. In larval insects or nymphs, delayed growth of the last instars or nymphal stages have been observed, often resulting in temporal segregation of emergence (Macan, 1965; Tudorancea & Green, 1975; Malas & Wallace, 1977; Bengtsson, 1981; Sweeney & Vannote, 1981; Brittain, 1982). Hildrew & Edington (1979) showed that two congeneric hydropsychid caddisflies avoided coexistence by different microhabitat colonization of some instars. Hydropsychidae were also studied

by Muotka (1990) who showed them having different microhabitat preferences according to different larval stages. Minshall (1984) observed changes in spatial distribution of insects according to developmental stages. Altogether, between egg and adult, the growing insects may live through many different feeding modes, behaviour or habitat niches (Winterbourn, 1971; Resh, 1979; Palmer *et al.*, 1993). These changes according to development allow them to reduce competition if resources are scarce.

In a previous paper (Bänziger *et al.*, subm.), we demonstrated differences in densities of several invertebrate taxa between the edge and the centre of macrophyte beds. The question arose whether these differences in density could be related to larval instar or size class distribution.

The purpose of the present study was to test the following hypotheses in a *Potamogeton pectinatus* L. bed of the littoral zone of Lake Geneva: i) distribution of insects in macrophyte beds changes according to larval instar or size class; and ii) congeneric species living in the same macrophyte bed differ in size and/or timing of larval instars.

## MATERIAL AND METHODS

The samples were taken in a *Potamogeton pectinatus* L. bed near Corsier (46°16' N, 6°12' E) in the littoral zone of Lake Geneva, Switzerland.

Samples were taken by scuba diving at a depth of 3.0 - 3.5 m in the edge, in the centre and adjacent to the macrophyte bed. The edge was defined as the margin of the bed characterised by lower macrophyte stem density, the presence of more filamentous algae (depending on the season) and by shorter shoots than in the centre of the bed. This corresponded to the 2 m wide outer belt of the macrophyte bed. Macrophyte density in the centre of the bed was 80 stems m<sup>-2</sup> at maximum density, i.e. in July. The (arbitrarily) 2 m wide area around the macrophyte bed, consisting of sediment, was defined as the adjacent sediment.

Macrophyte samples were taken from May through to November 1994, adjacent sediment was sampled from May to July. When the macrophytes senesced - from October to November - sampling was carried on in the plant underlying sediments and the remains of the *Potamogeton* bed. Collections were made using different sampling gears depending on the substrate:

Collections of fully grown macrophytes were made using a sampler modified after Gerking (1957) with a surface area of 0.25 m<sup>2</sup> and a height of 1 m. When vegetation was less dense a frame of 0.0625 m<sup>2</sup> with an attached net was used. Each of the two sampling gears was lifted down on the macrophytes by a scuba diver, the plants were teamed out of the sediment and the sampler was closed: the Gerking-like sampler by a trap and the net by a string.

Sediments underlying the macrophyte bed were collected using corers covering an area of 0.005 m<sup>2</sup> and pushed 10 cm deep into the sediments. Adjacent sediments were collected inside a 0.25 m<sup>2</sup> frame using the same net as for vegetation samples.

In the laboratory, samples were thoroughly rinsed with tap water and the macroinvertebrates were retained in a 250 µm sieve. They were conserved in 4% formalin.

Seven insect species were retained for measurements: *Caenis horaria* (L.), *C. luctuosa* (Burm.) (Ephemeroptera), *Mystacides azurea* (L.), *M. longicornis* (L.), *Oecetis lacustris* (Pictet), *O. ochracea* (Curtis) (Trichoptera) and *Acentria ephemerella* (Denis and Schiffermüll.) (Lepidoptera) on the basis of their abundance in the samples, their identification and/or the availability of congeneric species.

Larvae of mayflies were assigned to size classes as they do not have easily distinguishable cohorts (Benke & Jacobi, 1986). The size classes of *Caenis* spp. and the instars of Trichoptera and Lepidoptera were assigned on the basis of head capsule widths (HCW) as they were often reported to be more reliable than body length in separating the different stages (Bradbeer & Savage, 1980; Bass *et al.*, 1982).

Measures of HCWs were made at their widest point including the eyes (Smock, 1980; Bass *et al.*, 1982). All measures were made with an accuracy of 0.025 mm using a dissecting microscope with a micrometer.

Head capsules widths of *Caenis* spp. were divided into 18 classes of 0.05 mm each (Table 1). Larvae of *Mystacides* spp. and *Oecetis* spp. were divided into five larval instars (Table 2). At instar I, genera could not be keyed to species, so they were termed "juveniles".

TABLE 1

Correspondance between size classes and head capsule widths (HCW) of *Caenis* spp.

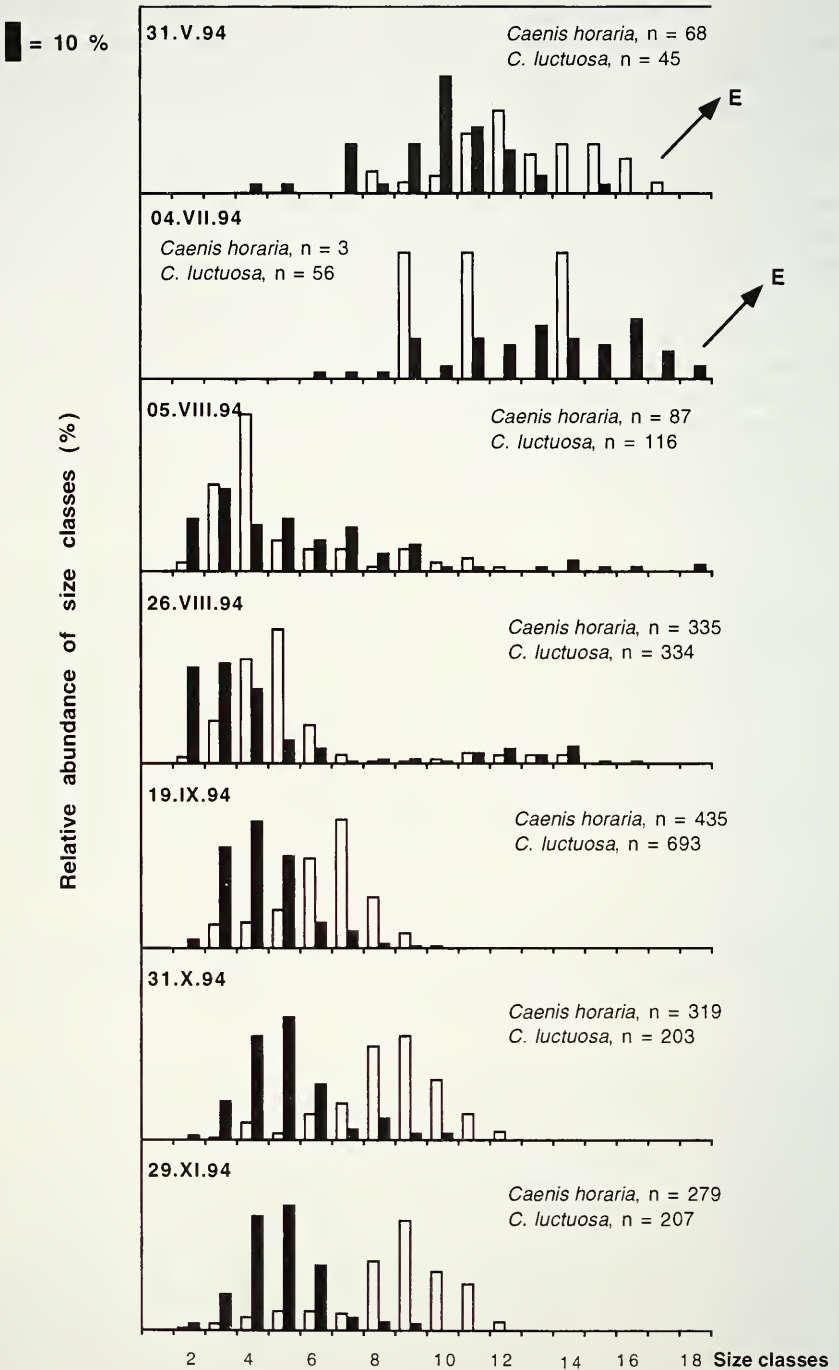
size classes	HCW of <i>Caenis</i> spp. (mm)	size classes	HCW of <i>Caenis</i> spp. (mm)	size classes	HCW of <i>Caenis</i> spp. (mm)
1	0.125 - 0.2	7	0.575 - 0.65	13	1.025 - 1.1
2	0.2 - 0.275	8	0.65 - 0.725	14	1.1 - 1.175
3	0.275 - 0.35	9	0.725 - 0.8	15	1.175 - 1.25
4	0.35 - 0.425	10	0.8 - 0.875	16	1.25 - 1.325
5	0.425 - 0.5	11	0.875 - 0.95	17	1.325 - 1.4
6	0.5 - 0.575	12	0.95 - 1.025	18	1.4 - 1.45

Data in the literature dealing with HCWs of *A. ephemerella* were scarce. Five instars were reported in the literature and Haenni (1974, 1980) identified the sizes of the different instars by collecting individuals in the field and by rearing them.

TABLE 2

Correspondance between instars and head capsule widths of *Mystacides azurea*, *M. longicornis*, *Oecetis lacustris* and *O. ochracea*.

instars	HCW of <i>Mystacides azurea</i> (mm)	instars	HCW of <i>M. longicornis</i> (mm)	instars	HCW of <i>Oecetis lacustris</i> (mm)	instars	HCW of <i>O. ochracea</i> (mm)
juv.	0.125 - 0.175	juv.	0.125 - 0.15	juv.	0.125 - 0.15	juv.	0.125 - 0.2
		II	0.175 - 0.2	II	0.175 - 0.2	II	0.25 - 0.3
III	0.2 - 0.275	III	0.25 - 0.325	III	0.25 - 0.35	III	0.375 - 0.475
IV	0.325 - 0.4	IV	0.375 - 0.475	IV	0.4 - 0.525	IV	0.625 - 0.825
V	0.5 - 0.675	V	0.575 - 0.75	V	0.675 - 0.875	V	0.95 - 1.275



Combining his results and our measurement yielded the following correspondence between HCWs and instars. Instar I: 0.2-0.3 mm; II: 0.325-0.5 mm; III: 0.525-0.775; IV: 0.8-0.925; V: 0.95-1.1 mm. The different instars are overlapping.

Emergence time of larvae and nymphs was based on numbers and size of the larvae and nymphs at the different sampling sessions.

## RESULTS

### COMPARISON OF GROWTH AND EMERGENCE TIME OF CONGENERIC SPECIES

The three pairs of congeneric species *Caenis* spp., *Mystacides* spp. and *Oecetis* spp. showed staggering in emergence patterns. This delay was already prepared for in autumn, *C. luctuosa*, *M. longicornis* and *O. lacustris* did stop growing from the middle of September, whereas, *C. horaria*, *M. azurea* and *O. ochracea* showed some growth until October - November.

According to the low numbers caught beginning of July, imagoes of *Caenis horaria* emerged between end of May and June. Juveniles appeared in the samples at the beginning of August, but their abundance was highest at the end of August (Fig. 1). At that time, the new generation extended over one month divided into two density peaks: the first one (low density) ranging from size classes 9 to 15 and the second one (high density) ranging from 2 to 8. The nymphs from the first (9-15) peak emerged by the middle of September. Nymphs of the second peak grew until the end of October. Most of them entered the winter period at size classes from 8 to 11.

*Caenis luctuosa* emerged later than *C. horaria*: at the beginning of July. Juveniles were collected in the samples at the beginning of August, as for *C. horaria*. The two species followed the same growth schedule (with two size class peaks at the end of August) until the middle of September. At that time *C. luctuosa* stopped growing, thus entering the winter period at size classes from 3-8 essentially.

Interpretation of the growth of *Mystacides azurea* was more difficult as sampling in May seemed to have bypassed the emergence of *M. azurea* (Fig. 2). *M. longicornis* emerged at the beginning of July and the first hatched larvae of *M. azurea* were ready to emerge at the beginning of August. Some *M. longicornis* larvae did also reach instar V at the end of August and emerged or disappeared until the middle of September. By the end of October, instars II to IV of *M. longicornis* and III and IV of *M. azurea* were present. *M. longicornis* did not grow further, whereas *M. azurea* was found from instars II to V at the end of November. Entering the winter in the last instar could preclude to an early emergence in spring.

In *Oecetis* spp., emergence time extended from the end of May through August for *O. ochracea*, while the emergence of *O. lacustris* was observed from beginning of July through August. Some of the first hatched larvae of the two species appeared at the

FIG. 1

Size classes and headcapsule widths of *Caenis horaria* (open columns) and *C. luctuosa* (dark columns). Black arrows: emergence.



beginning of August. *O. lacustris* did not grow further from the middle of September and overwintered in the instars II and III, while growth of *O. ochracea* lasted until the end of October and it overwintered in the instars III and IV.

#### GROWTH AND EMERGENCE OF *ACENTRIA EPHEMERELLA*

End of May was the end of the emergence period for *A. ephemerella* (Fig. 2). There were still some pupae found. At the beginning of July, the first new larvae

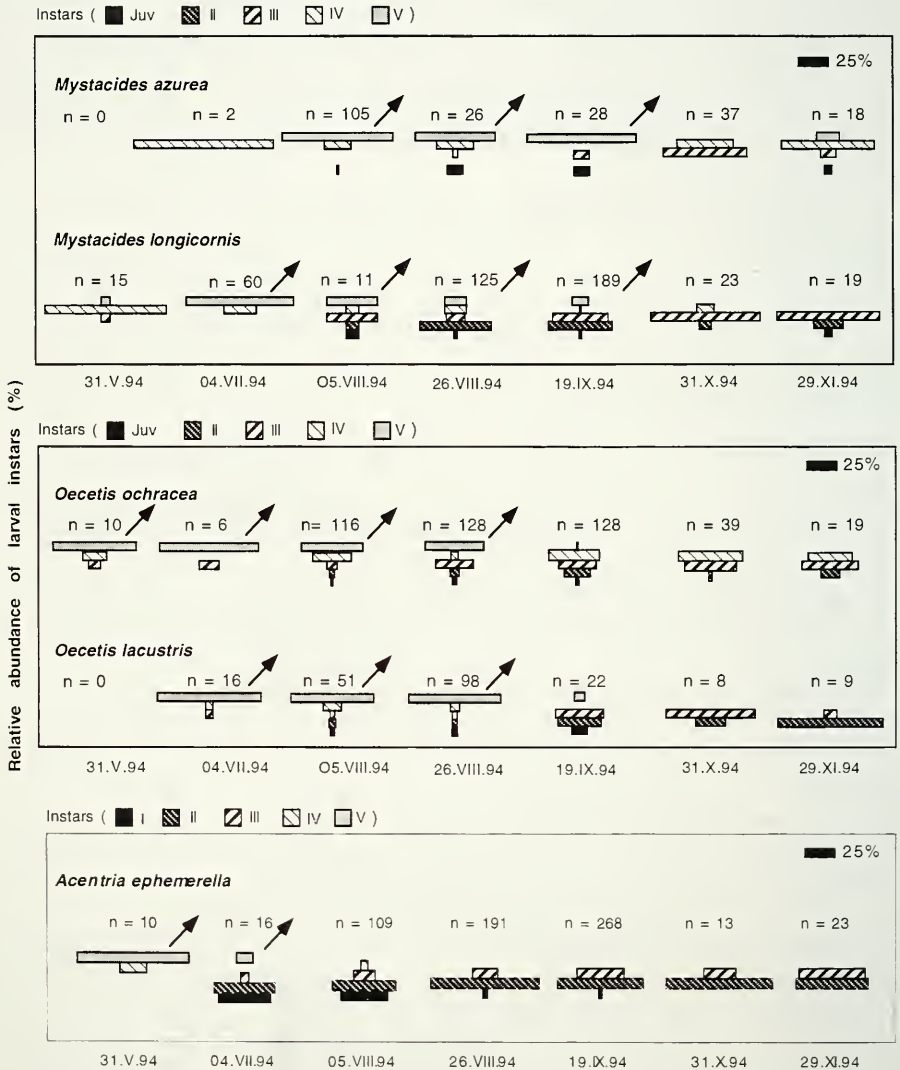


FIG. 2. Frequency of the instars of five insect species (*Mystacides azurea*, *M. longicornis*, *Oecetis lacustris*, *O. ochracea* and *Acentria ephemerella*). Juv.: indetermined juveniles of either *Mystacides* spp. or *Oecetis* spp. Black arrows: emergence.

appeared and at the beginning of August, all larval instars were present. The question remained whether instar V larvae were the first hatched of the 1994 cohort or the last hatched of the 1993 cohort. From August to November, young larvae grew to instar II and III and instar IV larvae disappeared. Abundance of instar II and III larvae was similar at the end of November.

#### SPATIAL DISTRIBUTION OF INSTARS

None of the seven insect species studied showed significant differences in relative abundance of the different instars or size classes between edge and centre of the macrophyte bed and the adjacent substrate. Our data and figures did however show higher relative abundances of instar V larvae on the plants (edge and centre), especially for *Oecetis* spp. and *Mystacides* spp. (Fig. 4).

*Caenis* spp. showed no tendency to colonize either plants or adjacent sediments (Fig. 3) and *Acentria ephemerella* was found quite exclusively on the plants (Fig. 5). *M. azurea* was slightly more abundant on the adjacent sediments and on the plants in the edge at the beginning of August, whereas *M. longicornis* was more abundant in the centre at instar V. Thus, it seemed to emerge in higher densities from the centre of the macrophyte bed than *M. azurea*.

*Oecetis* spp. were the only species which were quite abundant in the sediments. In May, they were mostly emerging from the sediments and in the subsequent sampling periods they were present in higher densities on the macrophytes, mainly at instar V. The bulk of emergence of *O. lacustris* originated from the edge, while *O. ochracea* emerged indifferently from the edge or the centre of the macrophyte bed.

*Acentria ephemerella* showed highest densities throughout the sampling sessions in the centre of the macrophyte bed, but at the end of May it was mainly found in the edge, besides of the pupae which were found in the centre. Only one individual was found at the beginning of August on the adjacent sediments.

#### DISCUSSION

The distribution of larval instars and size classes of the investigated congeneric insect species showed that temporal spacing of emergence was a major factor involved in their segregation. Indeed, several authors pointed out the importance of separated swarming in order to optimise mating success (Brittain, 1982). Moreover, the instar segregation already took place in autumn which allows to minimise resource depletion by similarly sized and similarly feeding larvae in winter when food sources are scarce. In *Oecetis* spp., this difference was enhanced by the lower size of *O. lacustris* (usually instar V larvae of *O. lacustris* had the size of instar IV larvae of *O. ochracea*). Size differences between species were lower for the two other congeneric species studied (*Mystacides* spp. and *Caenis* spp.).

The spacing of emergence involved that some species (i.e. *Oecetis* spp.) emerged before macrophyte resumed growth and they therefore did not need the presence of plants to complete their development. However, once the macrophytes were well established, *Oecetis* spp. and *Mystacides* spp. were found on macrophytes prior to

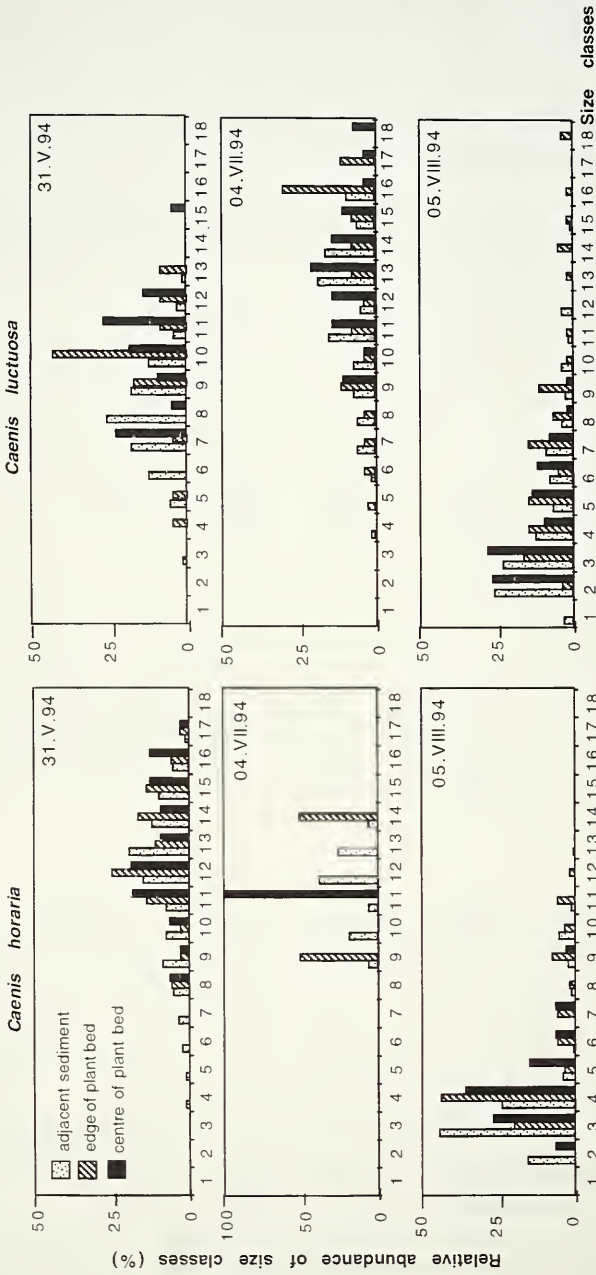


Fig. 3

Frequency of different size classes of *Caenis horaria* and *C. luctuosa* in the edge and in the centre of the macrophyte bed and on the adjacent sediment.



emergence. This may be ought to the advantage of the closer distance to the air-water interface which makes emergence easier and reduces the danger of predation (Rooke, 1984).

Among the seven species studied only two are known to mostly rely on macrophytes for feeding: *Mystacides longicornis* and *Acentria ephemerella*. Thus the main food resource in relation with macrophytes (i.e. plant tissue and periphyton) was not competed for to complete development (Berg, 1941; McGaha, 1952; Lepneva, 1966). The absence of difference in spatial distribution of congeneric taxa may either indicate that there is no spatial segregation or that it occurs at the microhabitat scale, as observed by Hildrew & Edington (1979) in rivers, rather than at the edge and centre scale of macrophyte beds. As Magdych (1979) and Müller-Liebenau (1956) reported, spatial segregation may take place between leaves, stems and roots at different heights (top, middle, bottom) of the plant.

Some instar I larvae of *Oecetis* spp. and *Mystacides* spp. may have been overlooked, thus biasing abundance data on the distribution of juveniles (Bass *et al.*, 1982).

*Caenis* spp. showed higher densities on the sediments. They emerged from any substrate and except for emergence and hibernation, their size classes were synchronised. The separation of the newly hatched nymphs into a fast growing (emerging after two months) and slow growing (hibernating) generation was already evidenced for *C. horaria* by Oertli (1992) in ponds of the Geneva area. Landa (1968) observed the same pattern for *C. horaria* during its study on central Europe Ephemeroptera. The variable life cycle patterns of Caenidae were reported by many authors (see Clifford, 1982). Thus, it is interesting to note at least identical patterns in different years and biotopes, but in the same area (i.e. Geneva), for one species.

*Oecetis* spp. illustrated the movement of larvae between the sediments and the macrophytes. Last instar larvae were more abundant on the sediments in May than in the subsequent sampling periods. It is likely that the larvae of *O. ochracea* did not have enough time (or food) to colonize the macrophytes early in the season and therefore they were still found on the adjacent sediments at the time of emergence. *O. lacustris* which emerged at the beginning of July, was able to emerge partly from the macrophytes. *O. ochracea* seemed to be clearly bivoltine, whereas *O. lacustris* showed a mainly univoltine pattern. These two species are at least partly predators so they are not relying on macrophytes for feeding (Mackay & Wiggins, 1970).

*M. longicornis*, which was found in substantially higher densities on macrophytes than on sediments (Bänziger, 1998), seemed to be synchronised with macrophyte growth. It emerged only once the macrophytes were established, and newly hatched larvae seemed to grow fast enabling them to emerge between the end of August and September. Thus this species showed a fast summer generation and a slower growing winter generation. *M. azurea* was more abundant on adjacent sediments than on macrophytes. It seemed to emerge early and grow slowly, as a limited number of larvae from the year emerged until autumn. Fast growth of *M. longicornis* and slow growth of *M. azurea* were also reported from Petersson (1989) in southern Sweden.

This study showed that closely related taxa with similar ecological niches may coexist in macrophyte beds at some developmental stages. Thus competition seemed

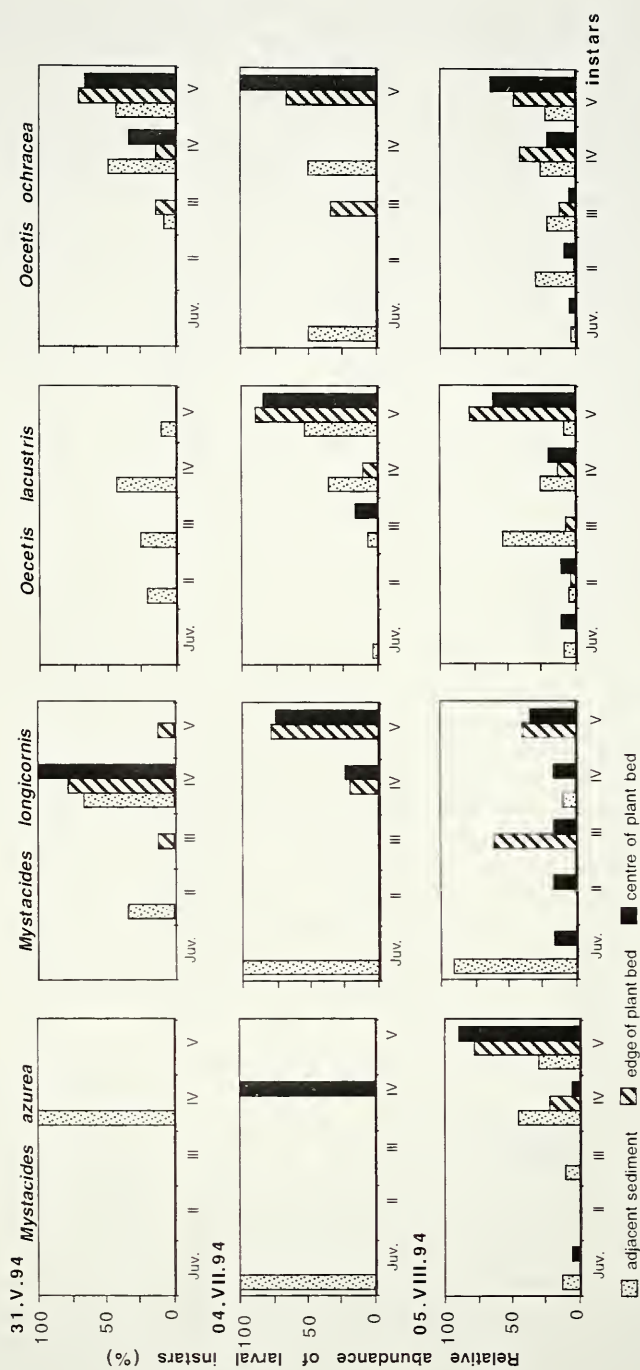


FIG. 4

Frequency of different larval instars of Trichoptera (*Mystacides azurea*, *M. longicornis*, *Oecetis lacustris* and *O. ochracea*) in the edge and in the centre of the macrophyte bed and on the adjacent sediment. Juv.: *Mystacides* spp. or *Oecetis* spp.

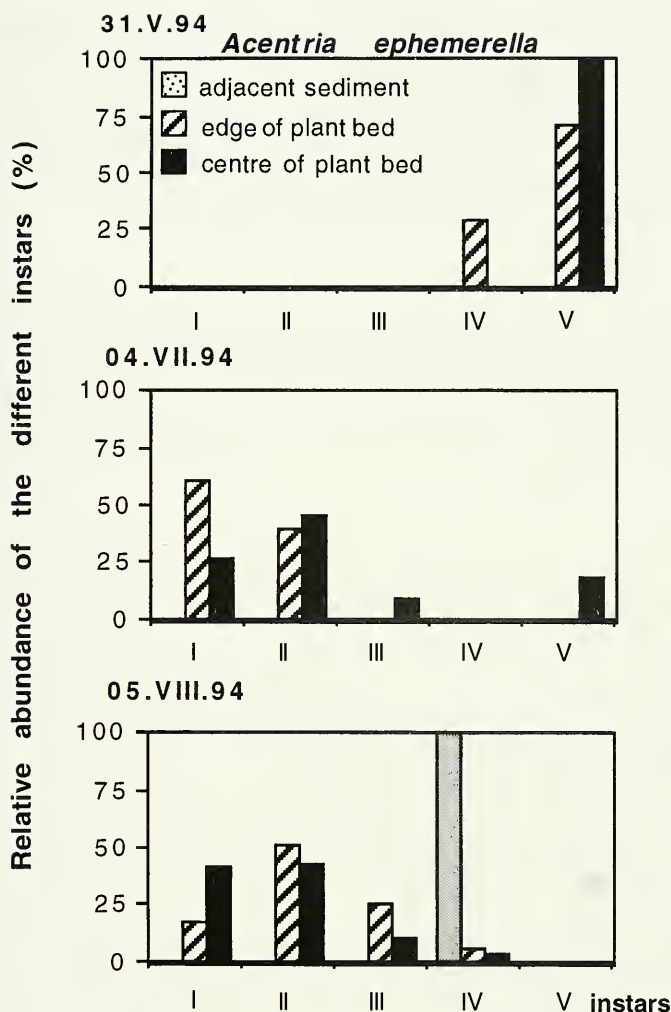


FIG. 5

Frequency of different larval instars of *Acentria ephemerella* in the edge and in the centre of the macrophyte bed and on the adjacent sediment.

not to be involved in species distribution during most of the invertebrate life cycle. Several papers dealing with invertebrate distribution on macrophytes in lakes conclude at an absence of competition in this habitat (Magdych, 1979). Hargeby (1990) explained this absence of competition by the yearly disturbance undergone by the invertebrates through the annual life cycle of the macrophytes. Each year colonization has to be resumed and competition has not enough time to take place (Pickett & White, 1985).

Temporal segregation occurred, however, between congeneric species before hibernation and during emergence. It may allow better resource partitioning when resources are scarce in winter and when maximum energy and food is needed just before emergence. Though there was a tendency for some taxa to live on the edge or on the adjacent sediment at small size classes and to be more abundant in the centre at the last instars or bigger size classes, this (statistically unconfirmed) result may be biased by the impact of predation at the edge on large and moving insects.

## ACKNOWLEDGEMENTS

I am grateful to all friends and colleagues who helped with the field work. In the laboratory, I thank B. Oertli for his stimulating discussions and D. Cambin who helped with HCW measurements. Special thanks to J.-P. Haenni who provided informations on *A. ephemerella*. I am grateful to B. Lods-Crozet and E. Castella for critical review of earlier drafts of this paper. Production of this paper was possible thanks to a grant from the Academic Society of Geneva.

## REFERENCES

- BÄNZIGER, R. 1998. Répartition spatio-temporelle des invertébrés aquatiques en relation avec la dynamique des herbiers littoraux (lac Léman). Thèse no 3035, *Université de Genève*, 120 pp. + annexes.
- BÄNZIGER, R., ZANINETTI, L. & LACHAVANNE, J.-B. (submitted). Edge effect in aquatic systems: macroinvertebrates in lake littoral macrophyte beds. *Aquatic Sciences*.
- BASS, J. A. B., LADLE, M. & WELTON, J. S. 1982. Larval development and production by the net-spinning caddis. *Polycentropus flavomaculatus* (Pictet) (Trichoptera), in a recirculating stream channel. *Aquatic Insects* 4: 137-151.
- BENGTSSON, B. E. 1981. The growth of some ephemeropteran nymphs during winter in a north Swedish river. *Aquatic Insects* 3: 199-208.
- BENKE, A. C. & JACOBI, D. I. 1986. Growth rates of mayflies in a subtropical river and their implications for secondary production. *Journal of the North American Benthological Society* 5: 107-114.
- BERG, K. 1941. Contributions to the biology of the aquatic moth *Acentropus nivens* (Oliv.). *Videnskabelige meddelelser fra Dansk naturhistorik forening* 105: 59-139.
- BRADBEE, P. A. & SAVAGE, A. A. 1980. Some observations on the distribution and life history of *Caenis robusta* Eaton (Ephemeroptera) in Cheshire and North Shropshire, England. *Hydrobiologia* 68: 87-90.
- BRITAIN, J. E. 1982. Biology of Mayflies. *Animal Review of Entomology* 27: 119-147.
- CLIFFORD, H. F. 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. *Quaestiones Entomologicae* 18: 15-90.
- GERKING, S. D. 1957. A method for sampling the littoral macrofauna and its application. *Ecology* 38: 219-226.
- HAENNI, J.-P. 1974. Biologie des Pyralidés (Lepidoptera) aquatiques sur la rive sud du lac de Neuchâtel. *Travail de Licence, Institut de Zoologie, Université de Neuchâtel*, 108 pp.
- HAENNI, J.-P. 1980. Contribution à la connaissance de la biologie des papillons aquatiques (Lepidoptera, Pyraloidea) sur la Rive Sud du Lac de Neuchâtel. *Bulletin de la Société Neuchâteloise de Sciences naturelles* 103: 29-43.
- HARGEBY, A. 1990. Macrophyte associated invertebrates and the effect of habitat permanence. *Oikos* 57: 338-346.

- HILDREW, A. G. & EDINGTON, J. M. 1979. Factors facilitating the coexistence of hydropsychid caddis larvae (Trichoptera) in the same river system. *Journal of Animal Ecology* 48: 557-576.
- LANDA, V. 1968. Development cycles of central European Ephemeroptera and their interrelations. *Acta Entomologica Bohemoslovaca* 65: 276-284.
- LEPNEVA, S. G. 1966. Fauna of the USSR. Trichoptera, vol. II. 2. Larvae and pupae of Intergripalpia. BYKHOVSKII, B. E. (ed.) Izdatel'stvo "Nauka", Moskva-Leningrad [Transl. by A. Mercado, Prof. O. Theodor for Israel Program for Scientific Translations Ltd.], 700 pp.
- MACAN, T. T. 1965. The fauna in the vegetation of a moorland fishpond. *Archiv für Hydrobiologie* 61: 18-310.
- MACKAY, R. J. & WIGGINS, G. B. 1970. Ecological diversity in Trichoptera. *Annual Review of Entomology* 24: 185-208.
- MAGDYCH, W. P. 1979. The microdistribution of mayflies (Ephemeroptera) in *Myriophyllum* beds in Pennington Creek, Johnston county, Oklahoma. *Hydrobiologia* 66: 161-175.
- MALAS, D. & WALLACE, J. B. 1977. Strategies for coexistence in three species of net-spinning caddisflies (Trichoptera) in second-order southern Appalachian streams. *Canadian Journal of Zoology* 55: 1829-1840.
- McAULIFFE, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65: 894-908.
- McGaha, Y. J. 1952. The limnological relations of insects to certain aquatic flowering plants. *Transactions of the American Microscopical Society* 355-381.
- MINSHALL, G. W. 1984. Aquatic insect-substratum relationships. Pp. 358-400. In: ROSENBERG, V. H. & RESH, D. M. (eds). The ecology of aquatic insects. Praeger Publ., New York.
- MÜLLER-LIEBENAU, I. 1956. Die Besiedlung der *Potamogeton*-Zone ostholsteinischer Seen. *Archiv für Hydrobiologie* 52: 470-606.
- MUOTKA, T. 1990. Coexistence in a guild of filter feeding caddis larvae: do different instars act as different species? *Oecologia* 85: 281-292.
- OERTLI, B. 1992. L'influence de trois substrats (*Typha*, *Chara*, feuilles mortes) d'un étang forestier sur la densité, la biomasse et la production des macroinvertébrés aquatiques. Thèse no 2557, Université de Genève. 283 pp.
- PALMER, C., O'KEEFE, J., PALMER, A., DUNNE, T. & RADLOFF, S. 1993. Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River, Eastern Cape, South Africa. I. Dietary variability. *Freshwater Biology* 29: 441-453.
- PETERSSON, E. 1989. Swarming activity patterns and seasonal decline in adult size in some caddis flies (Trichoptera: Leptoceridae). *Aquatic Insects* 11: 17-37.
- PICKETT, S. T. A. & WHITE, P. S. 1985. The ecology of natural disturbances and patch dynamics. Academic press Inc. Ltd., London, 472 pp.
- RESH, V. H., 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. *Journal of the Fisheries Research Board of Canada* 36: 290-311.
- ROOKE, J. B. 1984. The invertebrate fauna of four macrophytes in a lotic system. *Freshwater Biology* 14: 507-513.
- SMOCK, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology* 10: 375-383.
- SWEENEY, B. W. & VANNOTE, R. L. 1981. *Ephemerella* mayflies of White Clay Creek: bioenergetics and ecological relationships among six coexisting species. *Ecology* 62: 1353-1369.
- TUDORANCEA, C. & GREEN, R. H. 1975. Distribution and seasonal variation of benthic fauna in lake Manitoba. *Verhandlungen der Internationalen Vereinigung für Limnologie* 19: 616-623.
- WINTERBOURN, M. J. 1971. The life-history and trophic relationships of the Trichoptera of Marion Lake, British Columbia. *Canadian Journal of Zoology* 49: 623-635.